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The relation of climax vegetation to islands and peninsulas

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Lake Tsala Apopka, in the eastern part of Citrus County, Florida, is a shallow irregularly shaped sheet of water about 15 miles long and 5 miles wide, lying parallel to the Withlacooche River, just about on the line between the lime-sink and Gulf hammock regions.* Its bed and shores, like most of the surface of central Florida, are composed of sand presumably many feet in depth, covered with a little humus or peat in certain spots, but mostly fully exposed to the light. The topography in that part of the state is determined not so much by subaerial erosion as by irregular solution of the limestone which underlies the sand, and undulates in such a way as to give the lake an extremely sinuous outline.† This lake is so interspersed with islands and peninsulas that there is probably no point on its shores from which more than a few hundred acres of water can be seen at one time, even at its highest stage.

The country bordering the lake, on the west side (I have never been on the east side) is of the type known in Florida as "high pine land"; which means that it is covered with open forests of long-leaf pine, *Pinus palustris* (which is probably more abundant in central Florida than all other trees combined), with a fairly dense undergrowth of grasses and other herbs—most of them with small or narrow leaves—almost no shrubs or vines, and no mosses or lichens on the trees. Probably the most striking difference between long-leaf pine forests and other kinds is the scarcity of shade, and the other differences are in large measure correlated with this.

On January 21, 1909, when Lake Tsala Apopka was so low that one could make many short-cuts across its embayments (as is usually the case with Florida lakes in winter), I walked past or

* See Ann. Rep. Fla. Geol. Surv. 3: 221, 222. *pl. 16.* 1911.

† This peculiar topography is brought out very plainly on the Tsala Apopka topographic sheet of the U. S. Geological Survey (surveyed in 1893 and published in 1895, on a scale of about an inch to the mile).

across several of the peninsulas above mentioned, a few miles northeast of Inverness, and was much interested to find them all covered with rather dense forests of the "hammock"* type, contrasting strongly with the neighboring pine forests. As compared with the high pine land, equal areas on the peninsulas had trees much more numerous and herbs scarcer, both in individuals and species, and the trees all had broad leaves, giving a fairly dense shade. The composition of the peninsula forests, as determined by a few hours of rather hasty observation, seemed to be approximately as follows. (Trees, shrubs, and herbs are separated, and the species of each arranged as nearly as possible in order of abundance. Evergreens are indicated by bold-face type.)

TREES

Persea Borbonia
Magnolia grandiflora
Cornus florida
Osmanthus americana
Hicoria sp.
Quercus laurifolia
Quercus virginiana
Quercus geminata
Quercus Chapmani
Liquidambar Styraciflua
Ilex opaca

SHRUBS AND WOODY VINES

Batodendron arboreum
Cholisma ferruginea
Serenoa serrulata
Vitis rotundifolia
Gelsemium sempervirens
Phoradendron flavescens
Myrica cerifera
Aralia spinosa

HERBS

Tillandsia usneoides
Polypodium polypodioides
Epidendrum conopseum
Smilax pumila
Tillandsia tenuifolia?
Opuntia vulgaris
Mitchella repens
Rynchospora dodecandra

LICHENS

Trypethelium cruentum?

It is worth noting that in this list all but four of the trees,

* For definition of this term see Science II. 22: 400-402. 29 S 1905; Ann. Rep. Fla. Geol. Surv. 3: 98, 217. 1911.

all but two of the shrubs, and all the herbs, are evergreen; that two of the shrubs are vines, and half the herbs are epiphytes. It happens that all the herbs listed, except the last, have perennial stems above the ground; but a visit in summer would probably reveal a few herbs of the ordinary type, whose aerial parts die down in winter.

The broad leaves and consequent shade, the preponderance of woody plants over herbs, the absence of conifers, and the presence of several vines and epiphytes, are all characters of climax vegetation; but in the large proportion of evergreens, and a few other particulars, these hammocks differ considerably from the "mesophytic climax" forests a few hundred miles farther inland, where the soils are more clayey and the winters colder and wetter than in peninsular Florida. Forests very similar in aspect and composition to those just described, however, are found in many other parts of the coastal plain where deep sandy soils, mild dry winters and wet summers prevail, and they probably represent the climax type for those conditions of soil and climate. Although none of the species above listed are peculiar to Florida, about half of them are confined to the coastal plain or very nearly so.

The only apparent difference between the soil of the hammocks and that of the neighboring pine land was that due to the vegetation itself, namely, a small amount of humus (which is necessarily present in all hammocks and other shady upland forests) on the peninsulas. There is no reason to believe that the underlying limestone is any nearer to the surface on the peninsulas than elsewhere, and few of the plants listed are supposed to have any particular fondness for lime. Although I did not set foot on any of the islands in the same lake, I have no doubt that their vegetation differs little from that of the peninsulas.

Afterwards I observed a similar state of affairs at many other places in Florida, particularly in the lake region,* where many of the larger lakes have one or more narrow or narrow-necked peninsulas projecting out into them, with vegetation apparently always of the hammock type—if not already destroyed and replaced by orange groves or some other form of agricultural enterprise. And wherever islands occur in these lakes the vegetation

* See Ann. Rep. Fla. Geol. Surv. 3: 223. 1911.

seemed to be even denser if anything than on the peninsulas; which is just about what one would expect, whatever the cause of the approach to climax conditions on the peninsulas. From examining maps and literature, and from my own field notes for other parts of the country, I have been led to the conclusion that this relation between climax vegetation (the term "hammock" is not used so much outside of Florida) and peninsulas or islands is almost universal, at least in the coastal plain, and where the width of the peninsulas or islands lies between certain limits. A few examples in the coastal plain, from New Jersey southward, will serve to illustrate this principle.

Cape May, New Jersey, and neighboring beaches, from all accounts, are or have been noted for their fine white oaks, hollies, cedars, and some other trees which are rare or absent in the pine barrens a few miles farther north.*

On the Delaware peninsula, especially in Virginia, where it is narrowest, there are quite a number of species of trees and shrubs that are characteristic of hammocks farther south.† The whole coastal plain of Virginia north of the James River is cut up into peninsulas, and lacks many of the pine-barren plants which are found both in New Jersey and in North Carolina.‡ The original forests of this region (northern "Tidewater Virginia") must have been mostly hardwoods,§ and the timber and the accompanying humus-laden soil were doubtless among the attractions that determined the location there of some of the earliest English settlements in America, in the seventeenth century.

* See Ann. Rep. State Geol. N. J. 1891: 134-136; 1894: 262, 263; 1899 (Forests): 251, 252.

† See Torrey 9: 223. 1909. *Tillandsia usneoides*, a characteristic epiphyte of the Florida hammocks, has been reported from this same peninsula by Mr. Robert Ridgway (Bull. Torrey Club 8: 6. 1881), a fact that has been overlooked by many subsequent writers.

‡ See Torrey 7: 44, 45. 1907; 9: 217. 1909. Dr. Forrest Shreve, in his recent Plant Life of Maryland (pp. 85-88), has commented on the absence of some of the same species from the coastal plain of that state, which is also extensively dissected into peninsulas. Some notes on insular and peninsular vegetation on the western shores of Chesapeake Bay, by Dr. M. A. Chrysler, can be found on pages 187-189 of the same volume. According to C. D. Mell (Md. Geol. Surv., report on St. Mary's Co., p. 183, 1907) hardwoods originally predominated in this part of Maryland.

§ See Bull. Torrey Club 37: 422, 423. 1910.

The forests on the narrow sandy islands or "banks" which fringe the coast of North Carolina are said to consist almost entirely of angiospermous evergreens, including a large proportion of the same species already mentioned as growing in Florida.* Very few islands in the coastal plain north of South Carolina seem to have any pines on them.

The coast region of South Carolina, Georgia, and northeastern Florida, between the Santee and St. Johns rivers, is bordered by innumerable sandy islands, of diverse sizes and shapes, separated from each other and from the mainland by salt marshes and an intricate network of tidal channels; and these islands, or rather the portions of them not occupied by dunes and marshes, are wooded mostly with *Quercus virginiana* and its usual associates, pines being scarce or entirely absent on many of them.†

Paradise Key or Royal Palm Hammock, at the south end of the Everglades of Florida, is an island at high water, and is noted for its dense growth of tropical hardwoods, a few of which are not known to be arborescent anywhere else in the United States. Long Key, about half a mile away, is covered mostly with open pine forests, but at its eastern end, next to the channel which drains that end of the Everglades, there is a strip of hammock.‡

Among the Florida Keys proper, which are true islands, surrounded by salt water, pines are found only on a few of the largest ones,§ and the same seems to be true of the Bahamas, from all accounts. In both groups the smaller islands, except those small and low enough to be washed over by the waves, are as a rule covered with dense evergreen hammocks. In these Bahama and south Florida localities the soil is Pleistocene limestone instead of sand, and the pine is not *Pinus palustris* but *P. caribaea*;

* See Kerr, Tenth Census U. S. 6: 545, 561, 562, 564. 1884; Ashe, Bull. N. C. Geol. Surv. 6: 145-147. 1898; Kearney, Contr. U. S. Nat. Herb. 5: 271, 272. 1900.

† For a description of the vegetation of one of these islands on the coast of South Carolina see Coker, Torreya 5: 135-145. 1905.

‡ See Britton, Jour. N. Y. Bot. Gard. 5: 130-132. Jl 1904; Small, ibid. 5: 157-164. Au 1904; 8: 24. F 1907; 10: 49-54. Mr 1909; Harper, Fla. Review 4: 149, 152. Au 1910.

§ See Curtiss, Gard. & For. 1: 279, 280. 1888; Small, Jour. N. Y. Bot. Gard. 12: 153-157. 1911; also Ann. Rep. Fla. Geol. Surv. 3: 229. 1911.

but that is pretty closely related to *P. palustris* and very similar in its habits.*

On the Gulf coast of peninsular Florida, islands are rather scarce; but the coast of west Florida, Alabama, and Mississippi† is very similar in topography and vegetation to that of North Carolina, already referred to. Dr. Hilgard has described some sandy peninsular hammocks on the coast of Mississippi, differing from true peninsulas only in that the open water bordering them is partly replaced by marsh; and their vegetation, from his account,‡ is very similar to that already described.

Besides the peninsulas on the shores of lakes and oceans, there is another very common class, of worldwide distribution, formed by creeks and rivers. River peninsulas may be either at the confluence of two tributaries, or in "ox-bows" formed by meandering (and either kind may develop further into islands). Almost every one, in the southeastern United States at least, has noticed that such peninsulas, even above the reach of overflow, usually seem to have the richest soil in the neighborhood, and if not already cleared and cultivated, they are likely to bear some fine hardwood timber. This feature is of course more conspicuous in the long-leaf pine regions of the coastal plain, where the forests away from the streams are essentially of a pioneer type, than it is in the hardwood regions farther inland, where the contrast can never be so great.

Similar instances might be multiplied indefinitely;§ but the foregoing will probably suffice to show the universality of this relation between climax vegetation and small land areas wholly or partly surrounded by water or marshes, in our coastal plain. Almost the only exceptions to the rule seem to be those islands and beaches

* *Pinus caribaea* has been confused by recent writers on North American trees with *P. Elliottii*, a common and characteristic species of pine-barren ponds, branch swamps, etc., from South Carolina to Central Florida and Mississippi. They are not easily distinguished in the herbarium, but their ranges and habitats are quite different, *P. caribaea* being semitropical, and having about as little use for water as *P. palustris* has.

† For a description of the vegetation of some of the islands of Mississippi see Lloyd & Tracy, Bull. Torrey Club 28: 61-101. pl. 8-11. 1901.

‡ Geol. and Agric. Miss. 383, 384. 1860.

§ The reader who is sufficiently interested to follow up the matter can find descriptions of many peninsular hammocks in Bartram's Travels and other works of similar nature.

which are so narrow and so far from the mainland that they have no area sufficiently protected from the winds to allow humus to accumulate and hardwood forests to develop, or are so low that they are swept by the waves. Such beaches are found along the south shore of Long Island, on the coast of North Carolina, in the east and west Florida coast regions,* along the coast of Mississippi, and in various other places.

Now for the explanation of the phenomenon above described. Of the several hypotheses which readily suggest themselves, the least probable will be taken up and disposed of first.

In the case of islands and peninsulas bordered by large bodies of water (either fresh or salt), particularly some of the northernmost ones here discussed, it has been supposed by some that the peculiarities of their vegetation, and their agricultural advantages, are due to the temperature being kept more uniform by the proximity of the water, and especially to the greater exemption from frost enjoyed by such places. But the climax plants, or many of them at least, are not known or believed to be any more sensitive to heat and cold than the pioneer plants of the same regions are. In fact nearly all the hammock plants of central Florida are perfectly at home several hundred miles farther north,† and remote from large bodies of water. Furthermore, the temperature hypothesis would hardly explain the marked contrast between the peninsular hammocks of the Florida lakes and the pine forests which border the more gently curving shores of the same lakes; or the stream-fork peninsulas, where the width of the streams is often insignificant.

It might also be claimed that the islands and peninsulas are better watered than the pine forests near by; but this is not always true, and besides, the hammock plants are not especially moisture-loving, decidedly less so, for example, than bog plants, which are mostly of the pioneer class.

It might be true in some cases, such as on the sea islands and stream-fork peninsulas, that there is some fundamental difference in the soil. But in many or most of the instances cited, whatever difference there is in the soil can be ascribed to the vegetation

* See Ann. Rep. Fla. Geol. Surv. 3: 218, 226. 1911.

† This statement does not apply, however, to the hammock vegetation of south Florida and the Bahamas, mentioned incidentally above.

itself. Not only is shade conducive to the accumulation of humus and the retention of moisture, but the shade, humus, and moisture together favor the development of bacteria, fungi, worms, insects, and numerous other inconspicuous organisms, both animal and vegetable, which work on the soil in such a way as to increase the available nitrogen and otherwise improve it.* This, in short, is the regular way in which biotic succession (as defined by Cowles,† and distinguished from regional and topographic succession) proceeds, the world over.

For the Florida hammock peninsulas, if not for all the other cases referred to, the key to the situation can be expressed in a single word: FIRE. All the long-leaf pine forests of which I have any knowledge (and I have seen them in seven of the nine states and about 200 out of some 300 counties in which *Pinus palustris* is found), even the more or less isolated ones in the mountains of Georgia and Alabama, bear the marks of frequent fires. In prehistoric times these fires were doubtless set by natural agencies, probably mostly lightning, and each spot perhaps did not get burned over oftener than once in several years, on the average. Although fires may not be started by lightning on any one square mile oftener than once in several decades, a fire once started in the grassy carpet of an unbroken pine forest might easily spread over several square miles, so that every acre of such forest if not protected in some way would be likely to be burned over every few years. Forest fires are now usually set by man,‡ sometimes purposely and sometimes accidentally, but the increase in number of fires due to this cause has been partly counterbalanced by the numerous highways, clearings, etc., which serve as barriers to fire, so that the frequency of fire at any one point in the pine barrens may not be over two or three times as great as it was in prehistoric times, and the geographical distribution of forest fires in the southeastern states has probably not been changed materially.

* See in this connection a paper by J. W. Harshberger in *Science* II. 33: 741-744. 12 My 1911.

† Bot. Gaz. 51: 171-181. 1911.

‡ The Indians are supposed to have burned the pine woods for centuries before the white man arrived, and done it more regularly, but the differentiation between pine barrens and insular and peninsular hammocks probably antedates the whole human race.

It is pretty well known that long-leaf pine, after it is four or five years old, is less affected by fire than almost any other tree we have,* and in southern forests periodically swept by fire little else can grow but this pine and a great variety of more or less xerophytic, mostly perennial, herbs, among which various grasses are usually most abundant.

An island would ordinarily be exempt from fires except such as might originate on it, and consequently the smaller the island the less the chances of fire. On a peninsula, whether bordered by open water, marshes, or narrow streams, fire could approach from only one direction, and there would be many chances of its being stopped by rain, fallen logs, etc., before going very far down the peninsula, so that the frequency of fire in such places would be very much less than in unprotected forests where fire could approach from any direction.

On this theory it is easy to account for the origin of insular and peninsular hammocks. About half the species of plants listed above have fleshy fruits, and are presumably disseminated mostly by birds; and several others have nuts which may be carried considerable distances by rodents, such as squirrels. The seeds of such plants are doubtless being dropped all through the fruiting season in all sorts of places, and occasionally one will germinate, if it falls in the right kind of soil and does not encounter enemies or too much competition. In this way an island or peninsula which we might suppose for the sake of argument to have been originally covered with pine-barren vegetation would gradually become seeded with hardwoods.† The absence of fire would in time allow sufficient humus from the pioneer vegetation to accumulate to give the hardwoods a start, and the latter would grow up and finally make enough shade to prevent the reproduction of the pines and other pioneer plants, which are what foresters term intolerant, and will not germinate in dense shade.‡

* This point is discussed on pages 71-87 of a little book by G. Frederick Schwarz, entitled "The long-leaf pine in virgin forest," published in 1907.

† The ratio of fleshy-fruited trees to oaks and hickories should be somewhat greater on islands than on peninsulas, on account of the greater accessibility of the latter to mammals, but I have not yet investigated enough islands quantitatively to say whether this is true or not.

‡ In this connection Professor Bray's observations on the growth of *Pinus palustris* in eastern Texas (U. S. Bureau of Forestry Bull. 47: 22, 23. 1904) are of interest.

The relation between fire exemption and climax vegetation is reciprocal, for when the hardwoods are once well established the herbaceous vegetation under them is very sparse, and the humus is usually too damp or too thoroughly decomposed to burn readily. (There are of course all gradations between pioneer and climax forests, but I refer now to the extremes, and not to such intermediate stages as the common deciduous oak-hickory forests of the East and South, in which burning of the dead leaves in the fall, mainly through human agency, is a rather frequent occurrence.)

Outside of the long-leaf pine region or southern pine barrens (and south of the great northern coniferous forests, where fires are much more spectacular, and present a different set of problems) forest fires from natural causes, although they still occur, are less frequent, and the contrast between open and protected forests is consequently less marked. Peninsulas as wide as those of "Tide-water Virginia" would probably offer little hindrance to fire if their vegetation were of the pine-barren type, but they are just outside of the range of *Pinus rigida* on the one hand and *Pinus palustris* on the other, and the various hardwoods and short-leaf pines which prevail there* grow densely enough to make fires rather rare.

Although it is a little beyond the scope of this paper as indicated by the title, there is another piece of evidence in favor of the fire-protection theory of climax vegetation in the coastal plain that ought to be mentioned here. This theory furnishes a satisfactory explanation of another class of hammocks which has never been fully explained before: namely, those of the Altamaha Grit region of Georgia.† These are invariably located along creeks or rivers, and nearly always on the sandhill side of the stream. Their vegetation is very similar to that described above for the peninsulas of Lake Tsala Apopka. In former years I sought for the cause of these hammocks in the subsoil or the ground water; but it is clear now that protection from fire is the principal cause. For the pine-barren side of a stream, with its close carpet of wiregrass and

* See Bull. Torrey Club 37: 422, 423. 1910. The differences in vegetation on opposite sides of Hampton Roads are now a little easier to explain than they were before.

† See Ann. N. Y. Acad. Sci. 17: 98-102. pl. 16. 1906.

other inflammable herbs, is not usually sufficiently protected from fire to allow hammock vegetation to obtain a foothold there, while the sandhills, whose vegetation is so sparse that fires on them are very rare, furnish an excellent protection on that side. The trees in the swamp at the base of nearly every stream sandhill probably furnish the humus to start with, and the birds and squirrels bring the berries and nuts of the hammock plants, which gradually spread up the bare sandy slopes, making their own humus as they go.

The same theory also seems to explain why pine barrens approach nearer to salt marshes and salt water in Mississippi than in Georgia; a fact which I commented upon a few years ago* but could not account for at the time. The country within a few dozen miles of the coast in Georgia is considerably lower and flatter than that similarly situated in Mississippi, and tidal estuaries have encroached on it to a much greater extent, making many islands and narrow-necked peninsulas, as pointed out on a preceding page. In Mississippi the pine flatwoods are sparingly represented if at all, and undulating pine barrens like those of the Altamaha Grit region of Georgia come right down to the coast, the typical branch-swamp vegetation occurring within a few hundred yards of Mississippi Sound at Gulfport and elsewhere.

The shell hammocks on the coast of Alabama and Mississippi, described by Mohr † and Hilgard, ‡ must owe the peculiarities of their vegetation at least in part to the protection from fire afforded by the marshes or waterways by which they are invariably bordered.

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* *Torrey* 6: 201, 203. 1906.

† *Contr. U. S. Nat. Herb.* 6: 133. 1901.

‡ *Geol. & Agric. Miss.* 373, 374, 380. 1860; Tenth Census U. S. 6: 270, 271. 1884; *Soils* 495, 497. 1906.